THE PHYLOGENETIC DIVISION OF THE SUBFAMILY CEREOIDEAE, CACTACEAE[1]

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The subfamilies Pereskioideae K. Schum. and Opuntioideae K. Schum. of the family Cactaceae Lindl. are fairly well understood, but the subfamily Cereoideae K. Schum. (Schumann, 1898 and 1903) is so large and complex that its subdivision has puzzled all authors. The main reason for this difficulty in the past was that the descriptions of practically all genera belonging to this subfamily were completely inadequate. The internal structure of flowers, fruits, or seeds, all of extreme importance in recognizing relationships in the Cactaceae, had not been sufficiently examined. Thus all former attempts to subdivide this subfamily resulted in more or less schematic divisions which cut across the lines of evolution and united members of very different origin into polyphyletic units.

Therefore my first approach to this extremely difficult problem was a survey of the morphology of the Cactaceae (Buxbaum, 1936–1957c). These studies began with the more advanced branches of the Cereoideae. The more primitive genera were not at first available to me and their disposition remained very questionable. Nevertheless it was possible to delimit several of the tribes published by former authors as well as to point out the biphyletic origin of those cacti which Berger (1926) united into his Trichocerei. I discussed this provisional new phylogeny at the International Congress of the International Organization for Study of Succulent Plants (I.O.S.) at Zürich in 1951, and later this was published in provisional outline form (Buxbaum 1953a, 1956h). The details of the phylogeny of the tribe Echinocacteae (Euechinocactineae) were first published in 1951 (Buxbaum 1951b, 1951c, 1951h).

Since then it has been possible at least to delimit the extent of the tribes, and, in some instances, to indicate probable evolutionary lines. Nevertheless, much study still will be necessary to obtain a final knowledge of the evolution of the Cereoideae. This is because, for the most part, recently described "new genera" are so carelessly and insufficiently described that it is impossible to accept them. Since the Congress at Zürich I have been asked so often for an amplification of "my system" that I feel it necessary to publish at least the emended, or new, tribes and subtribes in accordance with the International Code of Botanical Nomenclature. To do this strictly in accord with the Code, it is necessary, unfortunately, to substitute new and different names for many of my provisional ones, but in each such case I have indicated my provisional name as a *nomen provisorium* in the synonymy.

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It should be emphasized that the classification within the tribes in most cases is not yet elaborated definitively and that several genera still are of doubtful position. In addition, this publication does not intend to give any judgment with regard to the validity or invalidity of many of the genera published hitherto. This can be done only in more detailed studies.

In order to interpret correctly the descriptive terminology used herein, readers are referred to my publications in English on the morphology of Cacti (Buxbaum 1950b, 1953c, 1955), where the specialized usage of such terms as pericarpel, receptacle, etc., will be found.

Backeberg overloaded his "Systematische Übersicht" with Latin-named taxa. Thus, in his second edition (1942), for the entire family Backeberg included 189 genera under 178 taxa above the rank of genus; for the Cereoideae alone he included 172 genera in 147 higher taxa. None of these was given a Latin diagnosis; thus all are *nomina nuda,* although he sometimes gave a suitable description in German. Backeberg pointed out that these Latin names were used only instead of numbers of a key, giving a characteristic by name; thus they are not true taxa and, indeed, many of them are adjectival and occur several times in different parts of the "system." Nevertheless, in his first edition, Backeberg (1938) put his name as author behind each of his names.

These names are ignored here except those of tribes, subtribes, and "nationes." As they are all *nomina nuda,* they could all have been ignored. However, so far as the name of any of these corresponds to a taxon used here, it is cited in the synonymy.

Even Berger (1926) did not give any description to his "Sippen" as he was aware of their provisional character. These, also, are in part cited here.

TRIBUS I.[2] **Leptocereae** trib. nov.

Echinocacteae K. Schum. p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose p.p. (1920), p. 1, Subtribe); *Leptocerei* Berg. nom. nud., p.p. (1926, p. 43, 95, Sippe); *Pfeifferae* Berg. nom. nud., p.p. (1926, p. 42, 95, Sippe); *Trichocerei* Berg. nom, nud., p.p. (1926, p. 49, 96, Sippe); *Leocerei* Backeb. nom. nud. (1938, Sippe; 1942, p. 42, Natio); *Cephalocerei* Backeb. nom. num., p.p. (1938, Sippe; 1942, p. 50, Natio); *Corryocerei* Backeb. nom. num., p.p. (1938, Sippe; 1942, p. 26, Natio); *Archicereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus): *Archicereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus).

[2]The method of synonym citation used throughout this paper is as follows. Under each tribe are listed all synonyms pertinent to the tribe or to any of its subtribes or linea. Each synonym is followed 1) by the author, 2) nomen nudum or nomen provisorium if applicable, 3) pro parte (p.p.) if the synonym applies only in part to the tribe in question, 4) the date and page, if any, of publication and rank of name (all in parentheses); for example: Trichocerei Berg. nom. nud., p.p. (1926, p. 42, 95, Sippe). By referring to the "Literature Cited," which includes all authors listed in the synonymy, the complete reference may be obtained. Under each subtribe any tribal synonyms pertinent to the particular subtribe in question are repeated, and are designated p.p., nom. nud., or nom. prov. as necessary. The date of publication and rank, however, are not repeated, since this information is available in the full synonymy listed under each tribe. No synonymy has been included for the linea except for Dr. Buxbaum's own applicable nomina nuda or nomina provisoria.—Ed.

Plantae habitu cereoideae modo primitivo ramosae nonnumquam prostratae vel adscendentes; costis plerumque haud numerosis, interdum 4 ad 8 iisque altis vel costis humilibus numerosis; floribus primitivissimis perianthio radiato parvo pericarpello et receptaculo perspicue cauliformibus brevibus squamis numerosis obsitis areolas spinosas, setosas vel saltem pilosas aut lanuginosas in axillis gerentibus. Genus typicum. *Leptocereus* (Berg.) Britt. & Rose.

Habit cereoid, the stems with branches arising basally or laterally and sometimes in a very primitive manner, sometimes prostrate or ascending; ribs usually few, sometimes only 4–8 and then very high, or numerous and low. Flowers very primitive; perianth radiate, relatively small; pericarpel and receptacle always shoot-like, short, the scales usually numerous and with spiny, bristly, or at least hairy or woolly areoles in their axils. South and Central America.

Genera (included for the present). *Armatocereus* Backeb., *Corryocactus* Britt. & Rose, *Erdisia* Britt. & Rose, *Eulychnia* Phil. (incl. *Philippicereus* Backeb.), *Facheiroa* Britt. & Rose (incl.? *Thrixanthocereus* Backeb and *?Vatricania* Backeb.), *Leocereus* Britt. & Rose, *Leptocereus* (Berg.) Britt. & Rose, *Neoraimondia* Britt. & Rose (incl. *Neocardenasia* Backeb.), *Neoabbottia* Britt. & Rose, *Samaipaticereus* Card., *Zehntnerella* Britt. & Rose.

This tribe contains several genera of very primitive character, especially with very primitive flowers. As these genera have not yet been examined sufficiently, it is not yet possible to arrange them phylogenetically. Some of the genera may possibly be transferred into one of the advanced tribes after further study. This tribe doubtless contains the oldest genera of the Cereoideae. The genus *Leptocereus* is probably the oldest of them.

TRIBUS II. **Hylocereae** trib. nov.

Rhipsalideae DC. (1828, p. 475, Tribus); *Echinocacteae* K. Schum, p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose, p.p. (1920, p. 1, Subtribe); *Hylocereanae* Britt. & Rose (1920, p. 183, Subtribe); *Epiphyllanae* Britt. & Rose (1923, p. 177, Subtribe); *Rhipsalidanae* Britt. & Rose (1923, p. 208, Subtribe); *Epiphylleae* Berg. nom. nud. (1926, p. 30, 95, Subtribus); *Hylocereae* Berg. nom. nud. (1926, p. 32, 95, Subtribus); *Leptocerei* Berg. nom. nud., p.p. (1926, p. 32, 95, Sippe); *Nyctocerei* Berg. nom. nud., p.p. (1926, p. 45, 95, Sippe); *Pachycerei* Berg. nom. nud., p.p. (1926, p. 59, 97, Sippe); *Pfeifferae* Berg. nom. nud., p.p. (1926, p. 42, 95, Sippe); *Corryocerei* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 26, Natio); *Heliocerei* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 45, Natio); *Nyctohylocerei* Backeb. nom. nud. (1938, Sippe; 1942, p. 24, Natio); *Heliohylocerei* Backeb. nom. nud. 1938, Sippe; 1942, p. 25, Natio); *Strophocerei* Backeb. nom. nud. (1938, Sippe; 1942, p. 24, Natio); *Phyllocacti* Backeb. nom. nud. (1938, Sippe; 1942, p. 23, Natio); *Phyllocactinae* Backeb. nom. nud. (1942), p. 23, Subtribus); *Hylocereideae* F. Buxb. nom. prov. (1953a, p. 6, Tribus); *Hylocereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus); *Hylocereinae* F. Buxb. nom. prov. (1953a, p. 6, Subtribus); *Hylocereineae* F. Buxb. nom. prov. (1956h, System 2, Subtribus); *Wittiae* F. Buxb. nom. prov. (1953a, p. 6, Linea); *Archirhipsalidae* F. Buxb. nom. prov. (*ibid.*, Linea); *Zygocacti* F. Buxb. nom. prov. (*ibid.*, Linea); *Eurhipsalidae* F. Buxb. nom. prov. (*ibid.*, Linea).

Frutices terrestres vel epiphytici multum ramosi arcuati adscendentes penduli vel scandentes; ramis paulum stabilibus teretibus costis numerosis humilibus, saepius costis paucis altis vel ramis trialatis vel phyllocladioideis vel teretibus ecostatisque, saepe articulatis; areolis apud genera primitiva spinosis, apud ea deductissima paulum modo lanuginosis; podariis plerumque rudimenta laminae gerentibus saepe glandulis nectariferis instructis; floribus ex areolis lateralibus saepe numerosissimis vel ex areolis ad apicem ramorum aggregatis, maximis aut minimis, nocturnis vel diurnis, albis, lutescentibus, viridescentibus, roseis vel coloratis, infundibuliformibus vel rotatis vel tubulatis plerumque radiatis, saepe receptaculo curvato pseudozygomorphis (apud Zygocactum vere zygomorphis); pericarpello apud genera primitiva squamoso et spinoso vel post anthesin spinas formante, apud genera deducta squamoso sine areolis, apud genera deductissima nudo; receptaculo breviter vel elongatissime infundibuliformi (apud subtribus Rhipsalinas paene absente) spinoso vel tantum squamoso vel plus minusve nudo, squamis receptaculi et pericarpelli saepe glanduliferis; perianthio plerumque conspicuo interdum basi eius tubum perianthii formante; staminibus fauce et tubo receptaculi modo variabili instructis numerosis vel reductione receptaculi paucis; pistillo crasso ramis stigmaticis permultis nonnumquam capitate cohaerentibus; funiculis ramosis (rarius simplicibus) saepe papillosis; fructu spinoso vel gibboso vel nudo laevique uviformi; seminibus magnis (apud Nyctocereum maximis) usque ad minimis, testa laevi vel foveolis interstitialibus punctata, perispermio absente, hypocotylo embryonis tenero, cotyledonibus magnis. Genus typicum. *Hylocereus* (Berg.) Britt. & Rose.

Shrubs of terrestrial habit, or in advanced genera shrubs of epiphytic, weak habit, then arching upward or leaning, hanging, or climbing, and much branched basally and laterally; branches sometimes terete with many low ribs or more frequently with only a few high ribs, or 3–5-alate to phylloclade-like, or sometimes terete and without ribs; both phylloclades and terete branches often articulate; branches usually developing aerial roots; areoles in primitive genera spiny, in advanced genera with only a little felt or a few hairs; podaria mostly with rudiments of laminae, often with an extranuptial nectary at the base of the lamina rudiment; cortical tissue with an abundance of large mucilaginous cells. Flowers lateral, often several from an areole which flowers repeatedly, or from aggregations of areoles at the tops of joints, very large (especially in subtribe Hylocereinae) to very small (subtribe Rhipsalinae, linea Rhipsales), night-blooming and white, pinkish, or yellowish, or day-blooming and bright colored to sometimes inconspicuous white, greenish, or yellowish, funnelform to widely rotate or tubular, radiate or sometimes pseudozygomorphic by bending of the receptacle (in *Zygocactus* zygomorphic); pericarpel in the more primitive genera scaly and spiny, in somewhat more advanced genera developing spines at maturity, in the more advanced genera without areoles, and finally in the most advanced genera nude and terete; receptacle in some primitive genera with spiny areoles in the

axils of scales, in the more advanced genera sometimes with very large scales, or in the most advanced genera more or less nude (scales when present very often with nectar glands below apex), short and massive-funnelform, or by extension of internodes very long (especially in *Epiphyllum*), in the subtribe Rhipsalinae reduced or almost totally absent, some of the most highly evolved genera with a true perianth tube; stamens variously distributed in the throat and along walls of the receptacle, sometimes only in upper part of the receptacle (*Epiphyllum*), sometimes a separate group around the pistil, mostly very numerous, fewer in the species with greatest reduction of receptacle, sometimes as few as 6 (*Rhipsalis cassytha* Gaertn.); style often very robust, the stigma lobes sometimes branched, usually numerous but sometimes in the most advanced genera few and small, or the stigma subcapitate; ovules arranged in bunches on branched funicles, these often bearing stiff papillae at the inner side of the bend (in the most advanced genera the funicles short and simple). Fruits fleshy, in the primitive genera with spines sometimes very numerous but fine, in the more advanced genera humped by the podaria of the scales, in the most advanced genera smooth and berry-like. Seeds very large (*Nyctocereus*) to very small (*Rhipsalinae*), smooth or spotted, without perisperm; embryo with large cotyledons and slender hypocotyl. Tropical and subtropical North, Central, and South America and West Indies, some *Rhipsalis* species secondarily distributed in tropical Africa, Madagascar, Zanzibar, Comoro Islands, and Ceylon.

Subtribus 1. **Nyctocereinae** subtrib. nov.

Echinocacteae K. Schum., p.p.; *Cereanae* Britt. & Rose, p.p.; *Nyctocerei* Berg. nom. nud., p.p.; *Leptocerei* Berg. nom. nud., p.p.; *Pachycerei* Berg. nom. nud., p.p.; *Corryocerei* Backeb. nom. nud., p.p.; *Heliocerei* Backeb. nom. nud., p.p.; *Heliohylocerei* Backeb. nom. nud.

Frutices terrestres ramis minus stabilibus vel arbores (Dendrocereus) ramosae, ramis alatis costis 3–5 altissimis vel eis humilibus teretibusque numerosis: floribus albis nocturnis (apud lineam Heliocerei rubris diurnis), pericarpello et plerumque etiam receptaculo spinosis (apud lineam Harrisiae tantum pilosis) radiatis (apud Aporocactum pseudozygomorphis), receptaculo tubiformi vel infundibuliformi. Genus typicum. *Nyctocereus* (Berg.) Britt. & Rose.

Habit terrestrial, the stems branching from the base or above; branches weak, or, if tree-like (as in *Dendrocereus*), partly pendent, terete with numerous low ribs or 3– alate with high ribs. Flowers usually night-blooming and white, sometimes (Linea Heliocerei) day-blooming and bright red, mostly radiate, rarely (in *Aporocactus*) somewhat zygomorphic; receptacle tubular to funnelform; areoles of pericarpel and receptacle usually spiny, sometimes (Linea Harrisiae) with hairs only.

Linea A. **Nyctocerei** linea nov.

Flores primitivissimi receptaculo et pericarpello spinosis. Genus typicum. *Nyctocereus* (Berg.) Britt. & Rose.

Flowers white, very primitive; pericarpel and receptacle very spiny.

Genera. *Nyctocereus* (Berg.) Britt. & Rose, *Brachycereus* Britt. & Rose and *Peniocereus* (Berg.) Britt. & Rose.

Linea B. **Acanthocerei** linea nov.

Flores magni, infundibuliformes, albi, pericarpello spinoso, receptaculo haud, vel in parte basali tantum spinoso. Genus typicum. *Acanthocereus* (Berg.) Britt. & Rose.

Flowers large, funnelform, white; pericarpel spiny; receptacle with spines only in basal part.

Genera. *Acanthocereus* (Berg.) Britt. & Rose, *Dendrocereus* Britt. & Rose.

Linea C. **Harrisiae** linea nov.

Flores magni, infundibuliformes, albi, areolis pericarpelli et receptaculi pilosis non spinosis. Genus typicum. *Harrisia*. Britt.

Flowers large, funnelform, white; areoles of pericarpel and receptacle with hairs only.

Genera. *Harrisia* Britt., *Eriocereus* (Berg.) Ricco.

Linea D. **Heliocerei** linea nov.

Flores diurni, rubri (exceptionibus paucis albis), magni, radiati vel positione staminum et receptaculo curvato pseudozygomorphi, pericarpello et receptaculo spinulosis. Genus typicum. *Heliocereus* (Berg.) Britt. & Rose.

Flowers day-blooming, red or (in one taxon) white, large, radiate to pseudozygomorphic by position of the stamens and/or bending of the receptacle; pericarpel and receptacle with fine spines.

Genera. *Heliocereus* (Berg.) Britt. & Rose, *Aporocactus* Lem.

Subtribus 2. **Hylocereinae** Britt. & Rose emend.

Echinocacteae K. Schum, p.p.; *Hylocereanae* Britt. & Rose; *Epiphyllanae* Britt. & Rose, p.p.; *Hylocereae* Berg. nom. nud.; *Epiphylleae* Berg. nom. nud., p.p.; *Nyctohylocerei* Backeb. nom. nud.; *Strophocerei* Backeb. nom. nud.; *Phyllocacti* Backeb. nom. nud., p.p.

Frutices ramosi elongati saepe scandentes, interdum repentes saepe epiphytici, ramis, angulatis vel alatis vel costatis rarius teretibus, radices aereas emittentibus; areolis plerumque spinosis; floribus magnis albis interdum roseis, pericarpello et receptaculo saepe crassissimis spinulosis squamosis interdum areolis solum pilosis, apud Hylocereum squamosis nudisque; perianthio radiato; fructu carnoso interdum permagno. Genus typicum: *Hylocereus* (Berg.) Britt. et Rose.

Habit elongated, vine-like, climbing, trailing or pendent, the stems branched, both stems and branches ribbed, fluted, or rarely flat, the joints emitting aerial roots, the areoles usually spiny. Flower mostly large, white or rarely pinkish; receptacle and pericarpel spiny and scaly, rarely the areoles bearing only a few hairs and wool, rarely without areoles (in *Hylocereus*); perianth limb regular. Fruit a fleshy, often large berry with a pulp, usually bursting upon maturity.

Genera. A. *Selenicereus* (Berg.) Britt. & Rose, *Cryptocereus* Alex., *Deamia* Britt. & Rose, *Strophocactus* Britt. & Rose. B. *Mediocactus* Britt. & Rose, *Wilmattea* Britt. & Rose, *Hylocereus* (Berg.) Britt. & Rose. C. *Werckleocereus* Britt. & Rose, *Weberocereus* Britt. & Rose, *Eccremocactus* Britt. & Rose. *Aporocactus* is now assigned to subtribe Nyctocereinae, linea Heliocerei.

No formal division into lines is proposed here, although the genera of this subtribe can be divided into three groups of presumably more or less closely related genera (A, B, C in list of genera above). When these genera are better known a formal subdivision may be possible. However, as Kimnach and Hutchison (1957) have pointed out, several of these genera may have to be reduced.

Subtribus 3. Epiphyllinae Britt. & Rose emend.

Epiphyllanae Britt. & Rose, p.p.; *Epiphylleae* Berg. nom. nud., p.p.; *Phyllocacti* Backeb. nom. nud., p.p.

Frutices epiphytici nonnumquam scandentes phyllocladiis variabilibus, eis saepe ex ramis non succulentis orientibus; floribus magnis radiatis nocturnis; receptaculo maxime elongato paulum squamoso, pericarpello squamoso, areolis in axillis squamarum interdum pilosis. Genus typicum. *Epiphyllum* Haw.

Habit epiphytic or climbing, with phyllodes of very variable shape, these sometimes branching from non-succulent shoots. Flowers conspicuous, radiate, night-blooming; pericarpel scaly, sometimes with hairs in the axils of the scales; receptacle much elongated, bearing only a few scales.

Genera. *Epiphyllum* Haw. (including *Marniera* Backeb.). Other genera included originally by Britton and Rose are here transferred to Hylocereinae, Disocactinae, and Rhipsalinae. See also Kimnach and Hutchison (1957).

Subtribus 4. **Disocactinae** subtrib. nov.

Epiphyllanae Britt. & Rose, p.p.; *Epiphylleae* Berg. nom. nud., p.p.; *Phyllocacti* Backeb. nom. nud., p.p.; *Wittiae* F. Buxb. nom. prov.

Frutices epiphytici phyllocladiis saepe ex ramis non succulentis orientibus; floribus magnis vel maxime simplificatis diurnis conspicue coloratis radiatis vel pseudozygomorphis; receptaculo tubulato vel infundibuliformi, plerumque squamoso, interdum petaloideo et in tubum perianthii transeunte; pericarpello squamoso vel fere nudo. Genus typicum. *Disocactus* Lindl.

Habit epiphytic, the phyllodes often branching from non-succulent shoots. Flowers large in some genera, and much simplified in others, day-blooming, bright colored, regular or pseudozygomorphic by bending of the receptable; pericarpel scaly to nearly naked; receptacle tubular to funnelform, mostly with scales, sometimes petaloid and transitional to a perianth tube.

Genera. *Nopalxochia* Britt. & Rose, *Lobeira* Alex., *Bonifazia* Standl. & Steyerm., *Chiapasia* Britt. & Rose, *Disocactus* Lindl., *Pseudorhipsalis* Britt. & Rose, *Wittia* K. Schum. *Lobeira* and *Bonifazia* will probably be reduced to *Nopalxochia* eventually. Kimnach and Hutchison (1957) reduce *Lobeira* to *Nopalxochia*.

Subtribus 5. Rhipsalinae Britt. & Rose emend.

Rhipsalideae DC.; *Rhipsalidanae* Britt. & Rose; *Pfeifferae* Berg. nom. nud., p.p.; *Epiphylloides* Backeb. nom. nud.; *Eurhipsalidae* F. Buxb. nom. prov.

Frutices epiphytici, rarissime terrestres, saepe radicantes, ramis angulatis, phyllocladioideis vel teretibus (in species unica opuntioideis) saepe articulatis; areolis lateralibus vel partim (interdum omnibus) aggregationem pseudoterminalem (pseudoareolam) formantibus; floribus ex areolis lateralibus vel ex aggregatione areolarum orientibus, diurnis, albidis lutescentibus vel coloratis, minimis, mediocribus, vel conspicuis, rotatis vel subinfundibuliformibus radiatis, in genere Zygocacto tantum zygomorphis; receptaculo plerumque brevissimo vel absente, pericarpello squamoso vel nudo, tereti vel anguloso, rarissime areolis setaceo-aculeatis instructo; foliis perianthii nonnumquam tubum perianthii formantibus; fructibus baccatis, seminibus parvis elongatis, hilo magno basali, embryonis cotyledonibus magnis, perispermio deficiente. Genus typicum. *Rhipsalis* Gaertn.

Habit rarely terrestrial, mostly epiphytic, the stems very often bearing aerial roots; branches angular, flattened, terete, or (in one species) *Opuntia*-like, often articulate; areoles lateral on the branches or the uppermost areoles of each joint aggregated at the top of joint and forming a large pseudoterminal pseudoareole. Flowers arising at lateral areoles or from pseudoterminal pseudoareoles, very small to quite large, day-blooming, whitish, yellowish, or colored, rotate or somewhat funnelform, radiate or rarely (in *Zygocactus*) zygomorphic; perianth a true tube in some genera; pericarpel terete or angular, scaly or nude, only very rarely bearing areoles with setaceous spines or hairs; receptacle mostly very short or absent. Fruits berry-like, globose, subglobose, or somewhat angular; pericarpel sometimes hidden in the branch tissue through the early growth of fruit (in other cases free from time of flowering). Seeds small, elongated; hylum large, basal; cotyledons large, the perisperm lacking.

Linea A. **Pfeifferae** linea nov.

Archirhipsalidae F. Buxb. nom. prov.

Ramis angulatis spinosis, haud articulatis; receptaculo brevissimo, pericarpello squamoso et spinoso, vel tantum squamoso. Genus typicum. *Pfeiffera* Salm-Dyck.

Branches angular, spiny, not distinctly articulate. Flower with receptacle much shortened; pericarpel spiny or scaly.

Genera. *Pfeiffera* Salm-Dyck, *Acanthorhipsalis* (K. Schum.) Britt. & Rose.

Linea B. **Schlumbergerae** linea nov.

Zygocacti F. Buxb. nom. prov.

Frutices ramis articulatis teretibus vel phyllocladioideis rarissime ex parte angulatis in specie unica opuntioideis; areolis partim prope apicem articulorum pseudoareolam formantibus; floribus ex pseudoareola orientibus (rare lateralibus), coloratis (rarissime albis), radiatis, in genere Zygocacto zygomorphis; pericarpello nudo; apud genus Erythrorhipsalis areolas pilosas gerente; receptaculo abbreviato apud genus Zygocacto in tubum perianthii transeunte. Genus typicum. *Schlumbergera* Lem.

Branches distinctly articulate, terete or flattened, rarely angular or (in one taxon) *Opuntia*-like, each joint bearing at the top an aggregation of areoles, these usually forming a large pseudoterminal pseudoareole. Flowers arising from pseudoterminal pseudoareoles, rarely also from lateral areoles, conspicuously colored, naked or (in *Erythrorhipsalis*) the pericarpel bristly; receptable shortened or (in *Zygocactus*) forming a true perianth tube.

Genera. *Erythrorhipsalis* Berg., *Hatiora* Britt. & Rose (including *Pseudozygocactus* Backeb.), *Rhipsalidopsis* Britt. & Rose (including *Epiphyllopsis* Berg., invalid name), *Schlumbergera* Lem., *Zygocactus* K. Schum. (including *Epiphyllanthus* Berg), (Buxbaum, 1957e).

Linea C. **Rhipsales** linea nov.

Eurhipsalidae F. Buxb. nom. prov. (1953a, p. 6, Linea.)

Ramis articulatis vel inarticulatis, teretibus vel phyllodioideis, rarius angulatis; floribus plerumque ex areolis lateralibus orientibus, radiatis, patenti-rotatis, minimis; receptaculo paene absente; pericarpello nudo. Genus typicum. *Rhipsalis* Gaertn.

Branches articulate or non-articulate, terete or flattened, rarely angular. Flowers usually from lateral areoles (if pseudoterminal then at the final joints of branches with very unequal joints), small to very small, regular, radiate; receptacle nearly absent.

Genera. *Rhipsalis* Gaertn., *Lepismium* Pfeiff.

The more natural a supergeneric taxon of advanced development is, i.e., the more it really corresponds to a widely branching part of the evolutionary tree, the less it is possible to give a "diagnosis" of it. Contrary to this, artificial taxa which are established with regard to "similarities" can easily be "defined," but very often these represent only equal stages of different branches rather than a phylogenetic unit. This is especially true for the tribe Hylocereae whose classification I have attempted above. In summary, it can be stated that although this tribe contains plants of extreme morphological differences [such as *Mediocactus megalanthus* (K. Schum.) Britt. & Rose with its gigantic flowers and *Rhipsalis cassytha* Gaertn. with the smallest flowers known in the family], it is nevertheless a very clear phylogenetic unit. Doubtless separating very early in evolution, probably from *Leptocereus*-like ancestors, this branch has taken a

very peculiar development, which has enabled it to occupy even the wet tropical zone. Some members have even reached the epiphytic stage.

In stem shape this tribe is dominated by two opposing tendencies: 1) the tendency towards diminution of the number of ribs, which may also become alate, so that the stems finally become phyllodes, and 2) the tendency towards total loss of ribs by confluence of low podaria into continuous cortical tissue, thus producing terete branches. Both of these tendencies can become manifest even at very different stages of evolution. For example *Werckleocereus imitans* Kimnach & Hutchison (1956) shows exactly the same pinnate habit of the phyllodes that occurs in *Cryptocereus anthonyanus* Alex. and in *Epiphyllum anguliger* (Lem.) Kelsey & Dayton. These three species of subtribe Hylocereinae are members of quite different lines of development within the subtribe, as already indicated. Terete branches occur in the very primitive genus *Peniocereus* (subtribe Nyctocereinae), in some species of *Weberocereus* (subtribe Hylocereinae), and finally in *Erythrorhipsalis, Hatiora,* and *Rhipsalis* (subtribe Rhipsalinae). In the flower at least three tendencies can be recognized: 1) the development of long-tubed, night-blooming, sphingine flowers, 2) the development of brightly colored, day-blooming, hummingbird flowers, 3) reduction and simplification of flowers. This third tendency can occur in combination with either of the first tendencies or separately.

Berger (1926), who had not yet recognized the tendency toward reduction in cacti, interpreted the simplified flowers as the most primitive ones. Therefore he did not recognize the connections, and so separated his "Rhipsalideae K. Schum." and Epiphylleae Berger as two subtribes. Today we can recognize the direct connection from a part of Berger's Sippe Nyctocerei (of his subtribe Cereae Berger) through the primitive subtribe Hylocereinae (= Berger's subtribe Hylocereae) to the three derived subtribes Epiphyllinae, Disocactinae, and Rhipsalinae. It has been necessary also to consider the day-blooming Epiphyllinae as another separate subtribe (Disocactinae), inasmuch as my recent examinations have made it evident that these have a separate origin.

TRIBUS III. **Pachycereae** trib. nov.

Echinocacteae K. Schum., p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose, p.p. (1920, p. 1, Subtribe); *Pachycerei* Berg. nom. nud. (1926, p. 59, 97, Sippe); *Gymnocerei* Berg. nom. nud., p.p. (1926, p. 55, 97, Sippe); *Pachycereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus); *Pachycereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus).

Arbores columnares permagnae simplices vel ramosae; floribus ex areolis immutatis vel ex pseudocephalio vel ex cephalio orientibus, radiatis, perianthio conspicuo vel parvo, albis vel rubescentibus interdum purpurascentibus; pericarpello plus minusve dense squamoso; axillis squamarum areolas lanuginosas, lanatas saepe setosas vel pilosas gerentibus, in generibus deductissimis axillis subnudis vel vere nudis; receptaculo pericarpello simili squamis decurrentibus plerumque minus quam pericarpello areolato; podariis squamarum pericarpelli et receptaculi saepe

nectar productentibus; staminibus infimis a basi receptaculi distantibus, protrusioni receptaculi saepe diaphragmam formante insertis, staminibus superioribus permultis tubo et fauce insertis; fructu saepe spinosissimo, plerumque longitudine irregulariter dehiscente. Genus typicum. *Pachycereus* (Berg.) Britt. & Rose.

Trees of large columnar habit, the trunk branching or simple. Flowers arising from normal areoles or from a pseudocephalium or cephalium, radiate, night-blooming or day-blooming; perianth conspicuous or small, white to reddish or purplish; pericarpel more or less densely scaly, areoles woolly, hairy, bristly, rarely spiny, but at least felted, only in the most advanced genera nearly or quite naked; receptacle similar to pericarpel, but the internodes elongated and thus the scales broadly decurrent and the areoles more reduced, podaria of scales very often producing nectar; lower stamens arising from a receptacular protrusion which often forms a diaphragm across the receptacular tube thus closing the nectar chamber; upper stamens numerous, arising from tube and throat of the receptacle. Fruit sometimes very spiny, bursting with irregular longitudinal splits. North America and Central America.

Genera (included for the present). *Pachycereus* (Berg.) Britt. & Rose, *Lemaireocereus* Britt. & Rose sensu lat. [including *Hertrichocereus* Backeb., *Isolatocereus* (Backeb.) Backeb., *Marginatocereus* (Backeb.) Backeb., *Neolemaireocereus* Backeb. (invalid name), *Polaskia* Backeb., *Ritterocereus* Backeb., *Stenocereus* (Berg.) Ricco.], *Neobuxbaumia* Backeb. emend. Dawson & F. Buxb. (Buxbaum, 1957a, cf. also Buxbaum, 1953b and 1954a), *Carnegiea* Britt. & Rose non Perkins, *Mitrocereus* (Backeb.) Backeb. (including *Backebergia* Bravo H.), *Cephalocereus* Pfeiff. [including *Haseltonia* Backeb., *Pilosocereus* Byles & Rowley (= *Pilocereus* K. Schum. non Lem.) p.p., Buxbaum, 1956f]. Genera incertae sedis: *Escontria* Rose and *Anisocereus* Backeb. These probably belong here.

This tribe has not yet been sufficiently studied. It cannot be maintained as circumscribed by Berger in his Sippe Pachycerei, and eventually must be emended further than is indicated in the preceding paragraphs. It is now clear that *Cephalocereus* Pfeiff., if interpreted as including only the two North American species *C. senilis* Pfeiff. and *C. Hoppenstedtii* K. Schum., certainly belongs here, also the newer genus *Neobuxbaumia* and at least a part of *Pilocereus* in the sense that Schumann used this name [*Pilocereus* K. Schum. non Lem. was proposed for conservation, but the proposal was rejected by the Nomenclature Committee of the International Botanical Congress. Byles and Rowley (1957) have recently proposed the name *Pilosocereus* to substitute for *Pilocereus* K. Schum. non Lem.]. According to my own studies (Buxbaum, 1956e), there is no strict necessity for separating the North American species of *Pilosocereus* from *Cephalocereus,* as they are closely related. Therefore these species ar included here under *Cephalocereus.*

The characters upon which Backeberg based the descriptions of the

genera which he separated from *Lemaireocereus* are quite insufficient to establish these genera, and further research is necessary. As indicated above, these genera are here included under *Lemaireocereus*. My last observations have shown that even *Lemaireocereus* [with *L. hollianus* (Weber) Britt. & Rose as type species] probably will not be retained, but will be placed in synonymy under *Pachycereus*.

TRIBUS IV. CEREAE Britt. & Rose emend.

Echinocacteae K. Schum. p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose, p.p. (1920, p. 1, Subtribe); *Gymnocerei* Berg. nom. nud., p.p. (as to "Cereoidei"; 1926, p. 55, 97); *Trichocerei* Berg. nom. nud., p.p. (1926, p. 49, 96, Sippe); *Cephalocerei* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 50, Natio); *Gymnocereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus); *Gymnocereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus).

Frutices semierecti, arcuati interdum prostrati, saepius arbores columnares erectae ramosae vel simplices; costis multis vel paucis interdum solum 3–5; floribus aut ex areolis immutatis aut ex pseudocephalio aut ex cephalio orientibus nocturnis saepe magnis campanulatis vel infundibuliformibus; pericarpello et receptaculo squamosis, squamis decurrentibus; axillis squamarum nudis (genere Jasminocereo excepto); staminibus infimis a basi receptaculi distantibus, plerumque protrusioni receptaculi diaphragmam non formante insertis, staminibus superioribus permultis tubo fauceque receptaculi insertis; fructibus carnosis dehiscentibus, funiculis seminum succosis. Genus typicum *Cereus* Miller.

Shrubs with slender half-erect, arching, or prostrate stems, varying to trees with large, columnar, upright stems, when trees the branches arising from the base, or from above a trunk, or the trunk simple; ribs many or few, sometimes (in some species of *Monvillea*) 3–5. Flowers arising from normal areoles or from a pseudocephalium or cephalium, nocturnal, radiate or somewhat bent and pseudozygomorphic, more or less slender-campanulate to funnelform, sometimes very large; pericarpel and receptacle bearing scales but lacking areoles in the scale axils (except in *Jasminocereus* which has a small amount of axillary felt which disappears on the fruit), in the more advanced genera the scales of pericarpel displaced upward onto the receptacle, the pericarpel thus becoming naked and showing only the decurrent scale bases; primary stamens arising above a distinct nectar chamber, but a diaphragm never formed; higher stamens arising from both wall and throat of the receptacle. Fruits fleshy, bursting, the funicles of the seeds juicy. South and Central America.

Genera. *Arrojadoa* Britt. & Rose non Mattf., *Austrocephalocereus* (Backeb.) Backeb. (including *Coleocephalocereus* Backeb., cf. Buxbaum, 1952b, c), *Browningia* Britt. & Rose (?including *Gymnanthocereus* Backeb.), *Cereus* Mill. [including *Monvillea* Britt. & Rose (cf. Werdermann, 1933), *Brasilicereus* Backeb., *Subpilocereus* Backeb.] *Jasminocereus* Britt. & Rose, *Stephanocereus* Berg., *Stetsonia* Britt. & Rose. Genera incertae sedis: *Lophocereus* (Berg.) Britt. & Rose and *Myrtillocactus* Cons. These probably belong here.

The study of this tribe is not yet completed. As it is now provisionally constructed it corresponds in general with the "Cereoidei" of Berger's Sippe Gymnocerei. Those genera which he lists in this Sippe as "Cactoidei" are now included in my Tribe VI, Notocacteae. In addition I have included here the genus *Browningia*.

TRIBUS V. **Trichocereae** trib. nov.

Echinocacteae K. Schum. p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose, p.p. (1920, p. 1, Subtribe); *Echinocereanae* Britt. & Rose, p.p. (1922, p. 3, Subtribe); *Echinocactanae* Britt. & Rose, p.p. (1922, p. 77, Subtribe); *Nyctocerei* Berg. nom. nud., p.p. (1926, p. 45, 95, Sippe); *Trichocerei* Berg. nom. nud., p.p. (1926, p. 49, 96, Sippe); *Cephalocerei* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 50, Natio); *Lobiviae* Backeb. nom. prov. (1942, p. 32, Natio); *Austroechinocacti* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 35, Natio); *Milae* Backeb. nom. nud. (1938, Sippe; 1942, p. 25, Natio); *Loxanthocerei* Backeb. nom. nud. (1938, Sippe; 1942, p. 27, Natio); *Trichocereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus); *Trichocereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus); *Trichocerei* F. Buxb. nom. prov. (1953a, p. 5, Subtribus); *Rebutinae* Donald (1955, p. 84, Subtribe); *Trichocereineae* F. Buxb. nom. prov. (1956h, System 3, Subtribus); *Loxanthocerei* Buxb. nom. prov. (1949, p. 10; 1953a, p. 5, Subtribus); *Loxanthocereineae* Buxb. nom. prov. (1956h, System 3, Subtribus).

Cactaceae simplices vel ramosae, columnares erectae vel prostratae vel brevicolumnares vel globosae, permagnae usque ad pusillae, costatae vel costis plus minusve in tubercula divisis; floribus insignibus albis vel coloratis radiatis vel ± pseudozygomorphis vel zygomorphis, receptaculo campanulato vel infundibuliformi vel tubiformi; pericarpello et receptaculo squamosis crispate pilosis (pericarpello rarissime spinuloso), apud genera deductissima pericarpello et receptaculo nudis; perianthio plerumque conspicuo, interdum (subtribus Borzicactinae) minuto sed receptaculo petaloideo-colorato; staminibus infimis prope basim receptaculi vel supra cameram nectariferam vel protrusione receptaculi insertis, interdum in pilos vel squamas staminodiales transformatis, staminibus secundariis parte inferiore et fauce receptaculi insertis, rarius in fauce absentibus; fructibus semisuccosis vel siccis lateraliter vel circumscisso dehiscentibus, interdum non dehiscentibus sed desintegrescentibus; seminibus testae typo verrucoso, apud genera deducta saepe testa laevi foveolis interstitialibus punctata, habitu variabilibus. Genus typicum. *Trichocereus* (Berg.) Ricco.

Stems simple or branching, globular to columnar, erect to prostrate but not climbing, large to dwarfish; stems and branches ribbed, in the most advanced genera the ribs more or less divided into tubercles. Flowers conspicuous, white or colored, radiate or (in Borzicactinae) more or less zygomorphic; perianth conspicuous or (in some Borzicactinae) small with scale-like segments, but then the receptacle petaloid and colored; pericarpel and receptacle with numerous usually acuminate scales, the axils with wool and crisped long hairs or occasionally with fine spines but then these only on the pericarpel, in the most advanced taxa the pericarpel and receptacle naked; receptacle campanulate to funnelform or

tubular; primary stamens inserted variously: 1) near receptacle base, leaving only a small nectar-furrow below, or 2) inserted at various heights so that the nectar chamber is limited indistinctly ("diffuse nectar chamber"), or 3) inserted on a more or less distinct protuberance which forms a closed nectar chamber; or the primary stamens sometimes transformed into staminodial hairs or scales; secondary stamens inserted only in lower part of tube and at margin of the receptacle, forming there a "hymen" which is absent only in the most advanced flowers. Fruits dry-fleshy, bursting laterally or opening with a circumscissile split or sometimes merely disintegrating. Seeds verrucose, in the highly advanced genera secondarily smooth and spotted, very variable in shape. South America.

This tribe is distinguished from the Tribe Notocacteae by 1) the stamen arrangement and 2) the basitony of the receptacular areoles (bristles never arise near the margin of the receptacle). Possibly it has developed from common ancestors with the Notocacteae, but its origin is not yet clear. The species descriptions are inadequate and consequently the genera are not yet sufficiently well defined; certainly several of the genera will be reduced to synonymy eventually.

Subtribus 1. **Trichocereinae** subtrib. nov.

Echinocacteae K. Schum. p.p.; *Cereanae* Britt. & Rose, p.p.; *Echinocereanae* Britt. & Rose, p.p.; *Nyctocerei* Berg. nom. nud., p.p.; *Trichocerei* Berg. nom. nud., p.p.; *Cephalocerei* Backeb. nom. nud., p.p.; *Lobiviae* Backeb. nom. prov., p.p.; *Austroechinocacti* Backeb. nom. nud., p.p.; *Trichocerei* F. Buxb. nom. prov.; *Trichocereineae* F. Buxb. nom. prov.

Plantae magnae columnares simplices vel ramosae, rarius globosae; floribus magnis radiatis campanulatis vel plus minusve infundibuliformibus, plerumque albis vel albidis nonnumquam coloratis; perianthio magno; camera nectarifera praesente vel absente. Genus typicum. *Trichocereus* (Berg.) Ricco.

Stems large and columnar or rarely globular. Flowers radiate, campanulate to funnelform; perianth large, mostly white or whitish, sometimes brightly colored; nectar chamber lacking or present; stamen insertion beginning at base of the receptacle or above a nectar chamber.

Genera. *Trichocereus* (Berg.) Ricco. (including *Helianthocereus* Backeb., *Leucostele* Backeb., *Roseocereus* Backeb., and *Weberbauerocereus* Backeb.), *Echinopsis* Zucc. [including *Pseudolobivia* (Backeb.) Backeb.; cf. Buxbaum, 1956f], *Haageocereus* Backeb. (including *Neobinghamia* Backeb. and *Peruvocereus* Akers, cf. Buxbaum 1952a), *Arthrocereus* Berg. [including *Setiechinopsis* (Backeb.) de Haas], *Espostoa* Britt. & Rose (including *Pseudoespostoa* Backeb.); cf. Buxbaum, 1952b, c), *Soehrensia* Backeb., *Acanthocalycium* Backeb.

Subtribus 2. Rebutinae Donald emend.

Echinocacteae K. Schum. p.p.; *Echinocereanae* Britt. & Rose, p.p.; *Trichocerei* Berg. nom. nud., p.p.; *Lobiviae* Backeb. nom. prov., p.p.; *Milae* Backeb. nom. nud.; *Rebutinae* Donald.

Plantae parvae vel pusillae, floribus radiatis, infundibuliformibus, coloratis (nonnullis albis exceptis); perianthio magno; receptaculo squamoso piloso, rarissime squamoso nudoque; pericarpello nonnumquam setaceo-spinuloso. Genus typicum. *Rebutia* K. Schum.

Plants small to dwarfish, flowers small, funnelform, radiate; perianth large, conspicuously colored or rarely whitish; pericarpel sometimes with small bristle-like spines; receptacle variously scaly, with hairs in the scale axils, or (in *Rebutia* K. Schum. subgen. *Rebutia*) the receptacle naked.

Genera (included for the present). *Lobivia* Britt. & Rose sensu lat. (including *Acantholobivia* Backeb., *Hymenorebutia* Fričˇ ex Buin., *Sulcorebutia* Backeb.), *Rebutia* K. Schum. [including *Aylostera* Speg., *Cylindrorebutia* Fričˇ & Kreuz (invalid), *Digitorebutia* Fričˇ & Kreuz ex Buin., *Mediolobivia* Backeb., *Pygmaeolobivia* Backeb.], *Chamaecereus* Britt. & Rose (Buxbaum, 1957d), *Mila* Britt. & Rose.

Because of intermediate species, the delimitation of genera in this group is difficult and still unsatisfactory. This is true especially for the genus *Lobivia,* which therefore is considered here in its broadest sense.

SUBTRIBUS 3. **Borzicactinae** subtrib. nov.

Echinocacteae K. Schum. p.p.; *Cereanae* Britt. & Rose, p.p.; *Echinocactanae* Britt. & Rose, p.p.; *Trichocerei* Berg. nom. nud., p.p.; *Loxanthocerei* Backeb. nom. nud.; *Austroechinocacti* Backeb. nom. nud., p.p.; *Loxanthocerei* F. Buxb. nom. prov.; *Loxanthocereineae* F. Buxb. nom. prov.

Plantae columnares interdum brevicolumnares vel globosae; floribus elongato-infundibuliformibus vel tubiformibus (apud genus *Oroyam* campanulatis); receptaculo petaloideo-colorato, squamoso et piloso rarissime subnudo vel nudo, saepe curvato itaque floribus pseudozygomorphis vel zygomorphis; perianthio haud permagno saepe reducto minuto atque minutissimo; camera nectarifera numquam presente. Genus typicum. *Borzicactus* Ricco.

Habit columnar or short-columnar (globular only in highly advanced, high montane genera, as in *Oroya*). Perianth relatively small or even much reduced; receptacle conspicuously colored, elongate-funnelform or tubular (campanulate only in *Oroya*), often more or less zygomorphic, nectar chamber very distinct (hummingbird flowers).

Genera (included for the present). *Loxanthocereus* Backeb. (including *Maritimocereus* Akers & Buin.), *Borzicactus* Ricco. (including *Bolivicereus* Card., ?*Clistanthocereus* Backeb.), *Denmoza* Britt. & Rose, *Cleistocactus* Lem. (Buxbaum 1956d), *Seticereus* Backeb., *Oreocereus* (Berg.) Ricco., *Morawetzia* Backeb., *Arequipa* Britt. & Rose, *Matucana* Britt. & Rose, *Oroya* Britt. & Rose.

TRIBUS VI. **Notocacteae** trib. nov.

Echinocacteae K. Schum. p.p. (1898, p. 46, Gruppe); *Echinocereanae* Britt. & Rose, p.p. (1922, p. 3, Subtribe); *Cactanae* Britt. & Rose (1922, p. 216, Subtribe); *Echinocactanae* Britt. & Rose, p.p. (1922, p. 77, Subtribe); *Erianthi* Berg. nom. nud., p.p. (1926, p. 68, 97, Sippe); *Gymnocerei* Berg. nom. nud., p.p. (as to "Cactoidei";

1926, p. 55, 97, Sippe); *Austroechinocacti* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 35, Natio); *Boreoechinocacti* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 54, Natio); *Cephalocacti* Backeb. nom. nud. (1938, Sippe; 1942, p. 53, Natio); *Pseudotrichocereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus); *Pseudotrichocereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus; here the tribe was further broken into the following provisional subtribes: *Notocactineae, Neoporteriineae, Parodiineae, Melocactineae, Gymnocalyciineae,* and an unnamed subtribe).

Plantae simplices vel basi ramosae, globosae vel applanatae, rarius elongatae brevicolumnares, nonnumquam pusillimae, costatae vel costis divisis, tubercula sub areolis posita formantibus; floribus ex areola quaque unico vel pluribus, vel ex pseudocephalio vel ex cephalio terminali orientibus; receptaculo campanulato vel infundibuliformi; pericarpello et receptaculo squamosis (apud genus Melocactum receptaculo nudo petaloideo), in axillis squamarum areoliferis vel rarius nudis; areolis pericarpelli et receptaculi valde pilosis rarissime lanatis spinosisque, superioribus plerumque setosis; staminibus supra sulcum nectariferum toto receptaculo usque ad faucem aequaliter insertis; foliis perianthii nonnumquam basi connatis; seminibus habitu variabilissimis typo testae verrucoso, variabili. Genus typicum. *Notocactus* (K. Schum.) Berger.

Stems simple or branching from base, globular to applanate, more rarely short-columnar, in the most advanced genera dwarfish; body ribbed, or the ribs divided into humps or even hump-like tubercles which occur below the areoles. Flowers solitary or several from the same areole, sometimes in a pseudocephalium or a terminal cephalium; pericarpel and receptacle covered with more or less numerous scales, the scales small, bearing in their axils much long wool, hairs, and, especially near the throat, stiff bent bristles or sometimes also fine bristle-like spines, sometimes (in *Gymnocalycium* and allies) the scales less numerous and naked in their axils, more rarely the flower areoles somewhat spiny or occasionally (in *Melocactus*) the flowers simplified to a "*Mammillaria*-shape", the petaloid receptacle lacking both scales and areoles; receptacle campanulate to funnelform, the tube sometimes elongate above margin of receptacle by union of basis of inner perianth segments, the stamens distributed equally from the distinct nectar furrow up to top of the receptacle. Seeds various in shape, the testa verrucose but the warts sometimes spine-like or secondarily flattened, the testa then smooth. South America (except *Astrophytum*).

Genera (included for present). *A. Eriosyce* Phil. *B. Austrocactus* Britt. & Rose, *Notocactus* (K. Schum.) Berg. (including *Brasilicactus* Backeb. and *?Eriocactus* Backeb.), *Islaya* Backeb. *C. Parodia* Speg., *Frailea* Britt. & Rose, *Astrophytum* Lem. (Buxbaum, 1951e, 1951g), *Blossfeldia* Werd. *D. Malacocarpus* Salm-Dyck non Fisch. & Mey., *Melocactus* Link & Otto. *E. Neoporteria* Britt. & Rose [including *Neochilenia* Backeb. (invalid name.), *Horridocactus* Backeb., and *Pyrrhocactus* Berg.], *Copiapoa* Britt. & Rose. *F. Gymnocalycium* Pfeiff. (according to personal communication from P. C. Hutchison in 1956, including

Weingartia Werd. and *Brachycalycium* Backeb.), *Neowerdermannia* Backeb., *Discocactus* Pfeiff.

In 1953 I first advanced a provisional grouping of genera for the Notocacteae, then called the Pseudotrichocereideae (Buxbaum, 1953a), and in 1956 (Buxbaum 1956h) I presented provisional subtribal names. My studies now indicate that these original groupings must be rearranged somewhat, but the research is not yet completed for final publication. For the present, I wish only to arrange the genera of the tribe into natural groups (A-F) as indicated in the preceding paragraph. The inclusion of *Neochilenia, Horridocactus,* and *Pyrrhocactus* under *Neoporteria* was first proposed in 1953 (Buxbaum, 1953a) and P. C. Hutchison (Verbal comm., 1956) has since confirmed the union of at least *Neochilenia* and *Horridocactus* with *Neoporteria.*

This tribe was confused by former authors with Berger's Trichocerei (Trichocereae of the present treatment). It is necessary to separate it because it clearly has had a separate evolution, possibly originating from *Corryocactus*-like ancestors. It is characterized by the acrotony of the receptacular areoles, the uppermost part of which are distinctly advanced, bearing more vigorous bristles than the lower ones, and by the arrangement of the stamens which differs distinctly from the arrangement in the Trichocereae.

TRIBUS VII. **Echinocereae** trib. nov.

Echinocacteae K. Schum. p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose, p.p. (1920, p. 1, Subtribe); *Echinocereanae* Britt. & Rose, p.p. (1922, p. 3, Subtribe); *Nyctocerei* Berg. nom. nud., p.p. (1926, p. 45, 95, Sippe); *Echinocerei* Backeb. nom. nud. (1938, Sippe; 1942, p. 42, Natio); *Heliocerei* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 45, Natio); *Echinocereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus); *Echinocereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus).

Frutices parvi plerumque ramis ascendentibus cylindricis teneribus, rarissime magni columnares repentes, vel plantae succulentissimae brevicolumnares vel globosae, erectae vel prostratae; ramis costatis plerumque spinosissimis, spinis saepe tenui-acicularibus et densissime positis; floribus conspicuis, diurnis, coloratis; pericarpello, plerumque etiam receptaculo squamosis spinosissimis (genere Rathbunia excepto); floribus radiatis apud genus Rathbunia zygomorphis. Genus typicum. *Echinocereus* Engelm.

Plants usually short-columnar or globular, the stem erect or prostrate, or plants low, much branched, shrub-like, the branches sometimes thin and weak, or rarely plants large, prostrate; branches ribbed, densely spiny, the spines strong to weak. Flowers conspicuous, day-blooming, colored, radiate (in *Rathbunia* zygomorphic); pericarpel and usually even the receptacle bearing scales, those of the pericarpel smaller, those of the receptacle larger and elongate with very spiny axillary areoles (except in *Rathbunia.*) North America.

Genera. *Bergerocactus* Britt. & Rose, *Machaerocereus* Britt. & Rose, *Rathbunia* Britt. & Rose, *Wilcoxia* Britt. & Rose (including *?Cullmannia* Dist.), *Echinocereus* Engelm.

The Echinocereae was first established by Britton and Rose as a subtribe (Echinocereanae). Besides *Echinocereus* they included in it *Lobivia* and its relatives, which are here assigned to Tribe Trichocereae, Subtribe Rebutinae. Berger did not recognize Britton and Rose's Echinocereanae, transferring the genera belonging in that group to form a day-blooming branch of his Nyctocerei. However, the connection with the Nyctocerei seems to be a very distant one, if it exists at all. Although much work still needs to be done on the Echinocereae, it seems to be well defined as presented here.

TRIBUS VIII. ECHINOCACTEAE K. Schum. emend.

Echinocacteae K. Schum. p.p. (1898, p. 46, Gruppe, = Tribus, p. 29); *Mamillarieae* K. Schum. (1898, p. 472, Gruppe); *Echinocactanae* Britt. & Rose, p.p. (1922, p. 77, Subtribe); *Coryphanthanae* Britt. & Rose (1923, p. 3, Subtribe); *Erianthi* Berg. nom. nud., p.p. (1926, p. 68, 97, Sippe); *Lepidanthi* Berg. nom. nud. (1926, p. 70, 98, Sippe); *Gymnanthi* Berg. nom. nud. (1926, p. 74, 98, Sippe); *Pseudomamillariae* Berg. nom. nud. (1926, p. 80, 98, Sippe); *Chasmatothelae* Berg. nom. nud. (*ibid.*, Sippe); *Coryphanthae* Berg. nom. nud. (*ibid.*, Sippe); *Mamillariae* Berg. nom. nud. (*ibid.*, Sippe); *Cochemieae* Berg. nom. nud. (1926, p. 80, 99, Sippe); *Pelecyphorae* Berg. nom. nud. (*ibid.*, Sippe); *Ariocarpi* Berg. nom. nud. (*ibid.*, Sippe); *Boreoechinocacti* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 54, Natio); *Euechinocactineae* F. Buxb. nom. nud. (1951b, p. 193, 197; 1951c, p. 98; 1951h, p. 31; 1953a, p. 3: Tribus); *Euechinocactidineae* F. Buxb. nom. prov. (1956h, System 4, Tribus); *Echinocacti* F. Buxb. nom. nud. (1951b, p. 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7: Linea); *Euechinocactineae* F. Buxb. nom. prov. (1956h, System 4, Subtribe); *Ramus* or *Ramis* [sic!] I F. Buxb. nom. prov. 1951b, p. 193, 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7); *Thelocactineae* F. Buxb. nom. prov. (1956h, System 4, Subtribus); *Thelocacti* F. Buxb. nom. nud. (1951b, p. 193, 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7; 1956h, System 4: Linea); *Strombocacti* F. Buxb. nom. nud. (1951b, p. 193, 197; 1951c, p. 100; 1951h, p. 33; 1953a, p. 7; 1956h, System 4; cf. also Buxbaum 1936, 1937: Linea); *Ramus* or *Ramis* [sic!] II F. Buxb. nom. prov. (1951b, p. 193, 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7); *Ferocactineae* F. Buxb. nom. prov. 1956h, System 4, Subtribus); *Ferocacti* F. Buxb. nom. nud. (1951b, p. 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7; 1956h, System 4: Linea); *Neobesseyae* F. Buxb. nom. nud. (1951b, p. 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7; 1956h, System 4: Linea); *Ramus* or *Ramis* [sic!] III F. Buxb. nom. prov. (1951b, p. 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7); *Coryphanthae* F. Buxb. nom. nud. (1951b, p. 197, Linea); *Coryphanthineae* F. Buxb. nom. prov. (1956h, System 4, Subtribe).

Cactaceae giganteae usque ad pusillae, brevicolumnares vel globosae vel depressae, costatae vel tuberculatae; tuberculis habitu variabili nonnumquam folioideis; areolis generum tuberculatorum plus deductorum vel in sulcam elongatum vel in areolam spinigeram et axillam florigeram divisis; areolis generum costatorum saepe glanduliferis; floribus ex margine superiore areolarum vel ex sulco tuberculi vel ex axillis orientibus, radiatis, rarissime zygomorphis (genus Cochemiea), diurnis; pericarpello crasso squamosissimo lanuginosissimo, receptaculo fere absente, vel floribus plus minusve campanulatis, receptaculo valde squamoso, areolis in flore absentibus vel apud genera deductissima pericarpello nudo et receptaculo petaloideo; fructo plus minusve carnoso saepe uveriformi; seminibus funiculo brevi simplici adnatis in quattuor lineis differentibus: 1)

testa dura nigra, levi, perispermio conspicuo (subtribus Echinocactinae), 2) testa verrucosa vel tuberculis testae secundariter laevis itaque foveolis interstitialibus punctata sublevi, perispermio praesente vel reducto etiam aborto (subtribus Thelocactinae), 3) testa foveolata vel reticulata nigra vel brunea, perispermio praesente apud genera deducta reducto atque aborto (subtribus Ferocactinae), 4) testa levi, brunea, celulis minimis perispermio praesente (subtribus Coryphanthinae); blastis succulentissimis cotyledonibus triangularibus apud genera deductissima maxime reductis. Genus typicum. *Echinocactus* Link & Otto.

Plants short-columnar, globular, or depressed, gigantic to small or dwarfish; stems ribbed or bearing short-conic to finger-like or leaf-like tubercles; areoles borne on the ribs or at or near the top of each tubercle or sometimes elongate and forming a groove on the upper surface of the tubercle, in the most advanced genera serially divided into a spine-bearing areole at the apex of the tubercle and a flower-bearing (floriferous) and sometimes shoot-bearing areole in the axil, in primitive genera sometimes with glandular spines. Flowers borne at the upper margin of areole or from the groove or in the axil, radiate or rarely zygomorphic, day-blooming; pericarpel scaly and woolly, the receptacle almost absent in the most primitive genera, more or less elongated-campanulate and distinctly scaly in the more advanced genera, and petaloid in the most advanced genera. Fruit more or less fleshy to juicy. Seeds on short and simple funicles which vary greatly in the different lines of evolution: 1) testa smooth, hard, black, the perisperm conspicuous (Echinocactinae, the most primitive subtribe); 2) testa verrucose, mostly black, the perisperm present or absent, the warts of the testa in most advanced genera becoming secondarily smooth but with more or less distinct spots between the testa cells, i.e., "spotted testa" (subtribe Thelocactinae); 3) testa "pitted" or reticulate, i.e., the testa with outer cell walls sunken in, the perisperm present or absent (subtribe Ferocactinae); 4) testa smooth, brown, with very small scales, the perisperm present (subtribe Coryphanthinae). Seedlings succulent, the cotyledons small, triangular, finally reduced to small humps. North America, to Venezuela in South America.

This tribe contains all the North American short-columnar or globular cacti with spineless flowers except *Astrophytum* (Buxbaum, 1951e, 1951g). It is a very clear-cut phylogenetic unit which has been thoroughly studied and is well understood except as to less important details in its phylogeny. The most primitive subtribe is the Echinocactinae.

Subtribus 1. Echinocactinae Britt. & Rose emend.

Echinocacteae K. Schum. p.p.; *Echinocactanae* Britt. & Rose, p.p.; *Erianthi* Berg. nom. nud., p.p.; *Boreoechinocacti* Backeb. nom. nud., p.p.; *Echinocacti* F. Buxb. nom. nud.; *Euechinocactineae* F. Buxb. nom. prov.

Echinocacteae giganteae brevicolumnares vel magnae globosae vel applanatae, costatae, spinosissimae; floribus pericarpello crasso squamosis-

simo pilosissimo (apud genus Homalocephalam parte inferiore nudo) seminibus magnis, testa nigra levi, rarius verrucosa vel minutissime reticulata, perispermio magno; embryonis cotyledonibus conspicuis triangularibus. Genus typicum. *Echinocactus* Link & Otto.

Plants short-columnar and gigantic to globular or applanate and conspicuous, ribbed, strongly spined. Flowers with the pericarpel thick, the scales numerous, with hairs and wool in their axils or (in *Homalocephala*) only at upper part; receptacle greatly reduced to almost absent. Seeds large; testa black, smooth or occasionally verrucose or somewhat reticulate; perisperm conspicuous. Embryo with cotyledons distinct, triangular.

Genera. *Echinocactus* Link & Otto, *Homalocephala* Britt. & Rose (possibly part of *Echinocactus*?)

Subtribus 2. **Thelocactinae** subtrib. nov.

Echinocacteae K. Schum. p.p.; *Mamillarieae* K. Schum. p.p.; *Echinocactanae* Britt. & Rose, p.p.; *Coryphanthanae* Britt. & Rose, p.p.; *Lepidanthi* Berg. nom. nud., p.p.; *Gymnanthi* Berg. nom. nud.; *Pseudomamillariae* Berg. nom. nud., p.p.; *Chasmatothelae* Berg. nom. nud.; *Pelecyphorae* Berg. nom. nud.; *Ariocarpi* Berg. nom. nud.; *Boreoechinocacti* Backeb. nom. nud., p.p.; *Ramus* or *Ramis* [sic!] F. Buxb. nom. prov.; *Thelocactineae* F. Buxb. nom. prov.

Echinocacteae parvae vel costatae costis saepe in tubercula divisis, vel tuberculatae; tuberculis nonnumquam folioideis, floribus receptaculo et pericarpello variabilibus, squamosis vel esquamosis, areolis absentibus; seminibus verrucosis, apud species nonnullas deductissimas secundariter levibus, foveolis interstitialibus punctatis; perispermio praesente vel absente. Genus typicum. *Thelocactus* (K. Schum.) Britt. & Rose.

Plants small, the ribs often divided into tubercles or humps, or the whole plant tuberculate, the tubercles sometimes leaf-like. Flowers very variable in shape; scales of the pericarpel and receptable, when present, mostly without areoles in the axils (occasional exceptions). Seeds black; testa verrucose, the warts in the most advanced genera becoming secondarily smooth (applanate) but with more or less distinct spots between the testa cells, i.e., "spotted testa"; perisperm present or absent.

Linea A. **Thelocacti** linea nov.

Thelocacti F. Buxb. nom. nud.

Plantae parvae globulares vel elongatae, costatae, costis in tubercula divisis vel tuberculatae; tuberculorum areolae apud genera deductissima in areolam spiniferam et axillam floriferam divisis; tuberculis nonnumquam sulcatis umquam folioideis; floribus prope apicem, vel ex margine superiore areolarum vel ex sulco vel ex axilla orientibus. Genus typicum. *Thelocactus* (K. Schum.) Britt. & Rose.

Plants small, globular or elongated, the ribs divided into tubercles or the plant tuberculate, finally reaching the "*Mammilaria* stage" with dimorphic areoles, the tubercles never leaf-like; spines strong, well-developed, sometimes hooked. Flowers borne near apex from the upper margin

of areoles or from the tubercle groove, or in the most advanced genera from the axils.

Genera (arranged in three natural groups). *A. Sclerocactus* Britt. & Rose, *Pediocactus* Britt. & Rose, *Utahia* Britt. & Rose. *B. Ancistrocactus* (K. Schum.) Britt. & Rose, *Hamatocactus* Britt. & Rose, cf. Buxbaum, 1951f (including *Glandulicactus* Backeb.), *Oehmea* F. Buxb. (Buxbaum 1951d), *Cumarinia* (Knuth) F. Buxb. *C. Echinomastus* Britt. & Rose, *Thelocactus* (K. Schum.) Britt. & Rose, *Neolloydia* Britt. & Rose, cf. Buxbaum, 1951d (including *Gymnocactus* Backeb.), *Rapicactus* F. Buxb. & Oehme, *Mammilloydia* F. Buxb. (Buxbaum 1951c. p. 64; 1951d).

Linea B. **Strombocacti** linea nov.

Strombocacti F. Buxb. nom. nud.

Plantae parvae globosae, elongatae vel applanatae rarissime costatae costis applanatis plerumque tuberculatis tuberculis saepe folioideis; spinis plerumque reductis nonnumquam papyrosis, saepe caduceis; floribus prope apicem ex margine areolarum vel ex sulco tuberculi vel ex axilla orientibus. Genus typicum. *Strombocactus* Britt. & Rose emend. F. Buxb.

Plants small, usually more or less globular, sometimes elongated, rarely with flattened and more or less divided (*Lophophora, Toumeya* p.p.) ribs, or more frequently tuberculate with the tendency to develop leaf-like tubercles; spines mostly reduced, sometimes papery, sometimes nearly lacking. Flowers near apex, from the top, groove, or axil of the tubercles.

Genera (arranged in closely related groups). *A. Toumeya* Britt. & Rose emend W. T. Marsh. [including *Turbinicarpus* (Backeb.) F. Buxb. & Backeb. and *Navajoa* Croiz.; according to W. Taylor Marshall (1947) and H. Bravo-H. and W. T. Marshall (1956, 1957) *Turbinicarpus* and *Navajoa* should be united with *Toumeya*], *Lophophora* Coult. *B. Strombocactus* Britt. & Rose emend. F. Buxb., *Aztekium* Boed. *C. Leuchtenbergia* Hook., *Obregonia* Frič & Berg., *Encephalocarpus* Berg., *Ariocarpus* Scheidw. (including *Roseocactus* Berg.), *Neogomesia* Castañ. *D. Epithelantha* Web. ex Britt. & Rose, *Pelecyphora* Ehrenb.

Subtribus 3. **Ferocactinae** subtrib. nov.

Echinocacteae K. Schum. p.p.; *Mamillarieae* K. Schum. p.p.; *Echinocactanae* Britt. & Rose, p.p.; *Coryphanthanae* Britt. & Rose, p.p.; *Lepidanthi* Berg. nom. nud., p.p.; *Pseudomamillarieae* Berg. nom. nud., p.p.; *Coryphanthae* Berg. nom. nud., p.p.; *Mamillariae* Berg. nom. nud., p.p.; *Cochemieae* Berg. nom. nud.; *Ramus* or *Ramis* [sic!] II F. Buxb. Nom. prov.; *Ferocactineae* F. Buxb. nom. prov.

Echinocacteae magnitudine variantes a plantis maximis brevicolumnaribus usque ad pygmaeis globularibus vel applanatis vel elongatis, costatis (costis apud genus Echinofossulocactum permultis lamellosis) vel tuberculatis; areolis generum tuberculatorum ovatis vel in sulcam elongatis vel in areolam spiniferam et axillam floriferam divisis; floribus squamosis vel nudis, pericarpello interdum petaloideo, fructibus carnoso-siccis vel uviformibus; seminibus foveolatis vel reticulatis, nigris vel bruneis, peri-

spermio praesente apud genera deductissima absente. Genus typicum. *Ferocactus* Britt. & Rose.

Plants short-columnar and large to globular or elongated and very small, ribbed in primitive genera, the ribs strong (*Ferocactus*) or thin and numerous (*Echinofossulocactus*), tuberculate in advanced genera; areoles in tuberculate plants elongate or dimorphic. Flowers scaly to naked, if naked, then the receptacle petaloid. Fruit dry-fleshy or juicy. Seeds black or in the most advanced species brown; testa cells with the outer cell walls sunken to produce a "pitted" testa, or if cells larger, the testa reticulate; perisperm present in the more primitive genera, absent in the more advanced genera.

Linea A. **Ferocacti** linea nov.

Ferocacti F. Buxb. nom. nud.

Plantae magnae, vel brevicolumnares vel globosae vel depresso-globosae, costatae (genera Coloradoa excepto), floribus ex margine areolarum orientibus, pericarpello et receptaculo squamoso. Genus typicum. *Ferocactus* Britt. & Rose.

Plants large, short-columnar to depressed-globose, ribbed or (in *Coloradoa*) tuberculate. Flowers borne at the margins of areoles; pericarpel and receptacle scaly.

Genera. *Ferocactus* Britt. & Rose (including *Brittonia* Houghton ex Armstr., invalid name), *Echinofossulocactus* Lawr., *Coloradoa* Boissev. & C. Davids.

Linea B. **Neobesseyae** linea nov.

Neobesseyae F. Buxb. nom. nud.

Plantae parvae vel pusillae, vel elongatae vel globosae vel depresso-globosae, rarissime brevicolumnares; areolis in sulcum extensis vel in areolam spiniferam et axillam floriferam divisis; floribus ex sulco vel ex axilla orientibus, receptaculo plus minusve petaloideo, squamoso vel nudo. Genus typicum. *Neobesseya* Britt. & Rose.

Plants small to dwarfish, elongate to depressed-globular, especially in some genera short-columnar in age, tuberculate; areoles elongate or dimorphic. Flowers borne from the groove or axil; receptacle more or less petaloid, scaly in the less advanced genera, naked in the highly advanced genera.

Genera. *Escobaria* Britt. & Rose emend. F. Buxb., 1951d, p. 78 (including *Escobesseya* Hester, invalid name), *Leptocladodia* F. Buxb. (Buxbaum, 1954c = *Leptocladia* F. Buxb. 1951 non Agardh, 1892, *Mamillopsis* (Morren) Britt. & Rose, *Neobesseya* Britt. & Rose (Buxbaum, 1951d), *Dolichothele* (K. Schum.) Britt. & Rose emend. Werderm. & F. Buxb. (Buxbaum, 1956g), *Pseudomammillaria* F. Buxb. (Buxbaum 1951c, p. 84; 1951d), *Mammillaria* Haw. non Stackh. [including *Bartschella* Britt. & Rose (Buxbaum, 1954d), *Chilita* Orcutt emend. F. Buxb. (1954b), *Ebnerella* F. Buxb., *Krainzia* Backeb., *Phellosperma* Britt. & Rose, *Porfiria* Boed., *Solisia* Britt. & Rose], *Cochemiea* (K. Brand.) Walt.

The seed of *Mammillaria simplex* Haw., type species of the genus, was not available to me for many years. According to the description it seemed to belong to the same type as the perisperm-containing *Mammillaria* seeds, and therefore the genus was placed in the Subtribe Coryphanthinae (Buxbaum 1950, 1951c, 1951h). Now the seed is recognized to have a pitted testa, indicating that the genus *Mammillaria* Haw. must be transferred to the Neobesseyae (Buxbaum, 1956a). This makes it possible to reunite again several of the separated genera with *Mammillaria,* as has been suggested as perhaps more desirable by Moran (1954). Nevertheless, some species of the genus, as presently conceived, must still be retained in the Coryphanthinae as they have the smooth testa and distinct perisperm of that subtribe, but research on this problem is not yet finished. Thus the genus *Mammillaria,* as herein circumscribed, is not homogeneous.

Subtribus 4. Coryphanthinae Britt. & Rose emend.

Mamillarieae K. Schum. p.p.; *Coryphanthanae* Britt. & Rose, p.p.; *Coryphanthae* Berg. nom. nud., p.p.; *Ramus* or *Ramis* [sic!] III F. Buxb. nom. Prov.; *Coryphanthae* F. Buxb. nom. nud.; *Coryphanthineae* F. Buxb. nom. prov.

Plantae magnitudinae media rarius parvae globosae, adultissimae interdum brevicolumnares, tuberculatae, areolis aut in sulcum tuberculi extensis aut in areolam spiniferam et axillam floriferam divisis, saepe glanduligeris; floribus ex sulco tuberculi vel ex axilla orientibus, squamosis vel nudis; receptaculo plus minusve petaloideo; seminibus levibus, bruneis, neque foveolatis neque verrucosis, interdum rugosis, testae cellulis minutissimis; perispermio semper praesente magno vel distincto. Genus typicum. *Coryphantha* (Engelm). Lem. sensu F. Buxb. (1951c. p. 96–97).

Plants medium-sized to small, globular to short-columnar, tuberculate; areoles extended to a groove or dimorphic. Flowers borne in the groove or axil. Seeds brown; testa smooth with very small cells, neither pitted nor spotted, sometimes shriveling; perisperm large or at least distinct.

Genus. *Coryphantha* (Engelm.) Lem. sensu F. Buxb.

At present this subtribe contains only the genus *Coryphantha* modified to include *Lepidocoryphantha* Backeb. (Buxbaum, 1951b, 1951c, 1956c). After further research the present species of *Mammillaria* which have a smooth testa and distinct perisperm undoubtedly will be transferred to the Coryphanthinae under a new generic name.

Summary of the Phylogenetic Division of the Cereoideae

TRIBUS I. LEPTOCEREAE F. Buxb.*[3]

Armatocereus Backeb.
Corryocactus Britt. & Rose
Erdisia Britt. & Rose
Eulychnia Phil. (incl. Philippicereus Backeb.)
Facheiroa Britt. & Rose (incl. ?Thrixanthocereus Backeb., ?Vatricania Backeb.)
Leocereus Britt. & Rose

[3]An asterisk marks each new name, each name in new status, and the name of each taxon whose circumscription is emended.

Leptocereus (Berg.) Britt. & Rose
Neoraimondia Britt. & Rose (incl. Neocardenasia Backeb.)
Neoabbottia Britt. & Rose
Samaipaticereus Card.
Zehntnerella Britt. & Rose

TRIBUS II. HYLOCEREAE F. Buxb.*

Subtribus 1. Nyctocereinae F. Buxb.*

Linea A. Nyctocerei F. Buxb.*
Nyctocereus (Berg.) Britt. & Rose
Brachycereus Britt. & Rose
Peniocereus (Berg.) Britt. & Rose

Linea B. Acanthocerei F. Buxb.*
Acanthocereus (Berg.) Britt. & Rose
Dendrocereus Britt. & Rose

Linea C. Harrisiae F. Buxb.*
Harrisia Britt.
Eriocereus (Berg.) Ricco.

Linea D. Heliocerei F. Buxb.*
Heliocereus (Berg.) Britt. & Rose
Aporocactus Lem.

Subtribus 2. Hylocereinae Britt. & Rose emend. F. Buxb.*

A. Selenicereus (Berg.) Britt. & Rose
Cryptocereus Alex.
Deamia Britt. & Rose
Strophocactus Britt. & Rose

B. Mediocactus Britt. & Rose
Wilmattea Britt. & Rose
Hylocereus (Berg.) Britt. & Rose

C. Werckleocereus Britt. & Rose
Weberocereus Britt. & Rose
Eccremocactus Britt. & Rose

Subtribus 3. Epiphyllinae Britt. & Rose emend. F. Buxb.*
Epiphyllum Haw. (incl. Marniera Backeb.)

Subtribus 4. Disocactinae F. Buxb.*
Nopalxochia Britt. & Rose
Lobeira Alex.
Bonifazia Standl. & Steyerm.
Chiapasia Britt. & Rose
Disocactus Lindl.
Pseudorhipsalis Britt. & Rose
Wittia K. Schum.

Subtribus 5. Rhipsalinae Britt. & Rose emend. F. Buxb.*

Linea A. Pfeifferae F. Buxb.*
Pfeiffera Salm-Dyck
Acanthorhipsalis (K. Schum.) Britt. & Rose

Linea B. Schlumbergerae F. Buxb.*
Erythrorhipsalis Berg.
Hatiora Britt. & Rose (incl. Pseudozygocactus Backeb.)

Rhipsalidopsis Britt. & Rose (incl. Epiphyllopsis Berg., invalid name)
Schlumbergera Lem.
Zygocactus K. Schum. (incl. Epiphyllanthus Berg.)

Linea C. Rhipsales F. Buxb.*
Rhipsalis Gaertn.
Lepismium Pfeiff.

TRIBUS III. PACHYCEREAE F. Buxb.*
Pachycereus (Berg.) Britt. & Rose
Lemaireocereus Britt. & Rose sensu lat. [incl. Hertrichocereus Backeb., Isolatocereus (Backeb.) Backeb., Marginatocereus (Backeb.) Backeb., Neolemaireocereus Backeb. (invalid name), Polaskia Backeb., Ritterocereus Backeb., Stenocereus (Berg.) Ricco.]
Neobuxbaumia Backeb. emend. Dawson & F. Buxb.
Carnegiea Britt. & Rose non Perkins
Mitrocereus (Backeb.) Backeb. (incl. Backebergia Bravo H.)
Cephalocereus Pfeiff. [incl. Haseltonia Backeb., Pilosocereus Byles & Rowley (= Pilocereus K. Schum. non Lem.) p.p.]
Genera incertae sedis:
Escontria Rose
Anisocereus Backeb.

TRIBUS IV. CEREAE Britt. & Rose emend. F. Buxb.*
Arrojadoa Britt. & Rose non Mattf.
Austrocephalocereus (Backeb.) Backeb. (incl. Coleocephalocereus Backeb.)
Browningia Britt. & Rose (?incl. Gymnanthocereus Backeb.)
Cereus Mill. (incl. Monvillea Britt. & Rose, Brasilicereus Backeb., Subpilocereus Backeb.)
Jasminocereus Britt. & Rose
Stephanocereus Berg.
Stetsonia Britt. & Rose
Genera incertae sedis:
Lophocereus (Berg.) Britt. & Rose
Myrtillocactus Cons.

TRIBUS V. TRICHOCEREAE F. Buxb.*

Subtribus 1. Trichocereinae F. Buxb.*
Trichocereus (Berg.) Ricco. (incl. Helianthocereus Backeb., Leucostele Backeb., Roseocereus Backeb., Weberbauerocereus Backeb.)
Echinopsis Zucc. [incl. Pseudolobivia (Backeb.) Backeb.]
Haageocereus Backeb. (incl. Neobinghamia Backeb., Peruvocereus Akers)
Arthrocereus Berg. [incl. Setiechinopsis (Backeb.) de Hass]
Espostoa Britt. & Rose (incl. Pseudoespostoa Backeb.)
Soehrensia Backeb.
Acanthocalycium Backeb.

Subtribus 2. Rebutinae Donald emend. F. Buxb.*
Lobivia Britt. & Rose sensu lat. (incl. Acantholobivia Backeb., Hymenorebutia Frič ex Buin., Sulcorebutia Backeb.)
Rebutia K. Schum. [incl. Aylostera Speg., Cylindrorebutia Frič

& Kreuz (invalid name), Digitorebutia Frič & Kreuz ex Buin., Mediolobivia Backeb., Pygmaeolobivia Backeb.]
Chamaecereus Britt. & Rose
Mila Britt. & Rose

Subtribus 3. Borzicactinae F. Buxb.*
Loxanthocereus Backeb. (incl. Maritimocereus Akers & Buin.)
Borzicactus Ricco. (incl. Bolivicereus Card., ?Clistanthocereus Backeb.)
Denmoza Britt. & Rose
Cleistocactus Lem.
Seticereus Backeb.
Oreocereus (Berg.) Ricco.
Morawetzia Backeb.
Arequipa Britt. & Rose
Matucana Britt. & Rose
Oroya Britt. & Rose

TRIBUS VI. NOTOCACTEAE F. Buxb.*

A. Eriosyce Phil.

B. Austrocactus Britt. & Rose
Notocactus (K. Schum.) Berg. (incl. Brasilicactus Backeb., ?Eriocactus Backeb.)
Islaya Backeb.

C. Parodia Speg.
Frailea Britt. & Rose
Astrophytum Lem.
Blossfeldia Werd.

D. Malacocarpus Salm-Dyck non Fisch. & Mey.
Melocactus Link & Otto

E. Neoporteria Britt. & Rose [incl. Neochilenia Backeb. (invalid name), Horridocactus Backeb., Pyrrhocactus Berg.]
Copiapoa Britt. & Rose

F. Gymnocalycium Pfeiff. (incl. Brachycalycium Backeb., Weingartia Werd.)
Neowerdermannia Backeb.
Discocactus Pfeiff.

TRIBUS VII. ECHINOCEREAE (Britt. & Rose) F. Buxb.*
Bergerocactus Britt. & Rose
Machaerocereus Britt. & Rose
Rathbunia Britt. & Rose
Wilcoxia Britt. & Rose
Echinocereus Engelm.

TRIBUS VIII. ECHINOCACTEAE K. Schum. emend. F. Buxb.*

Subtribus 1. Echinocactinae Britt. & Rose emend. F. Buxb.*
Echinocactus Link & Otto
Homalocephala Britt. & Rose

Subtribus 2. Thelocactinae F. Buxb.*

Linea A. Thelocacti F. Buxb.*

A. Sclerocactus Britt. & Rose
Pediocactus Britt. & Rose
Utahia Britt. & Rose

B. Ancistrocactus (K. Schum.) Britt. & Rose
Hamatocactus Britt. & Rose (incl. Glandulicactus Backeb.)
Oehmea F. Buxb.
Cumarinia (Knuth) F. Buxb.

C. Echinomastus Britt. & Rose
Thelocactus (K. Schum.) Britt. & Rose
Neolloydia Britt. & Rose (incl. Gymnocactus Backeb.)
Rapicactus F. Buxb. & Oehme
Mammilloydia F. Buxb.

Linea B. Strombocacti F. Buxb.*

A. Toumeya Britt. & Rose emend. W. T. Marshall [incl. Turbinicarpus (Backeb.) F. Buxb. & Backeb. and Navajoa Croiz.]
Lophophora Coult.

B. Strombocactus Britt. & Rose emend. F. Buxb.
Aztekium Boed.

C. Leuchtenbergia Hook.
Obregonia Frič & Berg.
Encephalocarpus Berg.
Ariocarpus Scheidw. (incl. Roseocactus Berg.)
Neogomesia Castañ.

D. Epithelantha Web. ex. Britt. & Rose
Pelecyphora Ehrenb.

Subtribus 3. Ferocactinae F. Buxb.*

Linea A. Ferocacti F. Buxb.*
Ferocactus Britt. & Rose (incl. Brittonia Houghton ex Armstr., invalid name)
Echinofossulocactus Lawr.
Coloradoa Boissev. & C. Davids.

Linea B. Neobesseyae F. Buxb.*
Escobaria Britt. & Rose emend. F. Buxb. (incl. Escobesseya Hester, invalid name)
Leptocladodia F. Buxb.
Mamillopsis (Morren) Britt. &Rose.
Neobesseya Britt. & Rose
Dolichothele (K. Schum.) Britt. & Rose emend. Werderm. & F. Buxb.
Pseudomammillaria F. Buxb.
Mammillaria Haw. non Stackh. (incl. Bartschella Britt. & Rose, Chilita Orcutt emend. F. Buxb., Ebnerella F. Buxb., Krainzia Backeb., Phellosperma Britt. & Rose, Porfiria Boed., Solisia Britt. & Rose)
Cochemiea (K. Brand.) Walt.

Subtribus 4. Coryphanthinae Britt. & Rose emend. F. Buxb.*
Coryphantha (Engelm.) Lem. (incl. Lepidocoryphantha Backeb.)

Cereoideae incertae sedis:

Azureocereus Akers & Johns.
Castellanosia Card.
Micranthocereus Backeb.
Neodawsonia Backeb.

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MOSSES OF CALIFORNIA VI. HALL NATURAL AREA AND MONO COUNTY

Leo Francis Koch

On the eastern slope of the Sierra Nevada, about five miles north of Tioga Pass and bordering Yosemite National Park, California, is the Harvey Monroe Hall Natural Area, the scene of the historic transplant experiments initiated by Dr. Hall and continued by J. Clausen, D. D. Keck, and W. M. Hiesey under the auspices of the Carnegie Institution of Washington. During the last decade, the writer has studied the collections of mosses made in this area by Dr. D. G. Catcheside in 1947 and by Dr. E. H. Ketchledge in 1953. I am indebted to Dr. Catcheside for placing his collection at my disposal, and to Dr. W. M. Hiesey for the loan of Dr. Ketchledge's collections. Dr. Malcolm A. Nobs of the Carnegie Institution at Stanford has been especially helpful in providing general information about the Natural Area and details of its topography and flora. Both Dr. Catcheside and Dr. Ketchledge kindly provided additional information and data about their collections.

The Harvey Monroe Hall Natural Area is part of the Toiyabe National Forest and includes approximately nine square miles, of which Mount Conness is the highest point at 12,556 feet above sea level. The area is severely glaciated and dissected by three hanging valleys which radiate in an easterly direction from the Sierran crest. The floors of these valleys are typically U-shaped, and alternate between alpine meadows and dry terminal moraines. According to Dr. Nobs, the habitats there are diverse, ranging from alpine bogs to places which are nearly desert-like and inhabited by sage-brush. *Pinus murrayana* Balf. and *P. albicaulis* Engelm. are dominant, the first at lower altitudes and on slopes with a southern exposure, and the second at higher altitudes and on slopes with northern exposure. Tree line is about 11,500 feet above sea level, and the alpine turf above it includes the caespitose *Salix petrophila* Rydb. as well as many "cushion plants." From the information available at the Carnegie Institution at Stanford, the vascular plants of the area include more than 330 species, of which 10 are pteridophytes and 6 are gymnosperms.

In this area, Dr. Catcheside and Dr. Ketchledge collected a total of 58 species of mosses, of which 5 appear to be the first authentic records from California: *Blindia acuta, Bryum muehlenbeckii, B. pallens, Campylium stellatum,* and *Mnium orthorrhynchum.* Dr. Howard A. Crum identified